Representations of the Body Surface in Areas 3b and 1 of Postcentral Parietal Cortex of Cebus Monkeys

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The somatotopic organization of postcentral parietal cortex was determined with microelectrode mapping methods in a New World monkey, *Cebus albifrons*. As in previous studies in macaque, squirrel and owl monkeys, two separate representations of the body surface were found in regions corresponding to the architectonic fields 3b and 1. The two representations were roughly mirror-images of each other, with receptive field locations matched for recording sites along the common border. As in other monkeys, the glabrous digit tips of the hand and foot pointed rostrally in the Area 3b representation and caudally in the Area 1 representation. Both representations proceeded in parallel from the tail on the medial wall of the cerebral hemisphere to the teeth and tongue in lateral cortex along the Sylvian fissure. Compared with the other monkeys, the tail of the cebus monkey, which is prehensile, was represented in a very large region of cortex in Areas 3b and 1. Like its close relative, the squirrel monkey, the representation of the trunk and parts of the limbs were reversed in orientation in both Area 3b and Area 1 in cebus monkeys as compared to owl and macaque monkeys. The reversals of organization for some but not all parts of the representations in cebus and squirrel monkeys suggest that one line of New World monkeys acquired a unique but functionally adequate pattern of somatotopic organization for the two adjoining fields.

INTRODUCTION

In a series of papers we have described the organizations of the 4 strip-like architectonic fields of the classical 'primary' region of postcentral somatosensory cortex of owl[12], macaque[9,15] and squirrel monkeys[19]. In all of these monkeys, separate representations of the body surface were found in architectonic Areas 3b and 1, while evidence was presented for additional representations of predominantly deep receptors in Areas 3a and 2. The organizations of the Area 3b and the Area 1 representations were determined in great detail, and general features of organization of the two fields became apparent. The two representations were in parallel proceeding from the tail to the oral cavity in a medial to lateral sequence across cortex, with the two representations forming approximately mirror-images of each other in organization from the 3b/1 border. In all monkeys, the glabrous digits of the hand and foot pointed rostrally in Area 3b and caudally in Area 1. In both owl and macaque monkeys, the representation of the trunk proceeded from dorsal midline to ventral midline in a rostrocaudal sequence across Area 3b and from ventral midline to dorsal midline in a rostrocaudal sequence across Area 1. Much to our surprise we found the reverse organization of the trunk representations in squirrel monkeys. The ventral midline of the trunk was found rostrally in Area 3b and caudally in Area 1, while the dorsal midline was found at the 3b/1 border. This suggests that each representation has several

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'sectors' or 'blocks' in which the basic somatotopic orientation can be independently determined. Furthermore, since the reversal in orientation of the 'trunk' sector of Area 3b in squirrel monkeys was matched by a reversal of the 'trunk' sector of Area 1 so that the organizations of these two fields maintained a mirror-image relation, the somatotopic organization of Areas 3b and 1 must be interdependent.

After finding the reversal of organization in squirrel monkeys, we wondered if this feature of somatosensory cortex is present in any other monkey. Because owl and macaque monkeys are not closely related, and because the organization of Area 3b found in these monkeys is typical of the primary somatosensory cortex of prosimians and a wide range of non-primate species[8], the organization in Area 3b of macaque monkeys and owl monkeys probably represents the basic mammalian plan, while the reversed organization in squirrel monkeys represents an evolutionary change. The change, we reasoned, might be restricted to squirrel monkeys, or it might have a longer evolutionary history and also be found in close relatives of squirrel monkeys. The taxonomic relationships of New World monkeys are not completely settled, but a close *Cebus-Saimiri* association has been postulated (e.g. refs. 3, 5 and 17). Thus, the organizations of Areas 3b and 1 in cebus monkeys was determined and compared with other monkeys.

Some of the present results have been briefly presented elsewhere[4].

MATERIALS AND METHODS

Electrophysiological cortical mapping experiments were conducted on 6 adult cebus monkeys, *Cebus albifrons*. Methods of animal preparation, recording and data analysis were similar to those used in previous studies of owl monkeys[12], macaque monkeys[15], and squirrel monkeys[19]. In brief, animals were initially anesthetized with ketamine hydrochloride (35 mg/kg, i.m.) and given supplementary doses (1/10 initial dose) as needed to maintain a surgical level of anesthesia. Body temperature was main-

tained at 37 °C. A large craniotomy exposed parietal cortex of one hemisphere. A dam of acrylic cement was formed around the craniotomy, and the well was filled with silicone fluid to protect the brain. The dura was reflected, and a high resolution photograph of the brain surface was taken and subsequently used to site electrode penetrations. Glass-coated platinum iridium microelectrodes with impedances of approximately 1–2 MΩ (1 kHz) were introduced in penetrations perpendicular to the cortical surface and advanced with a hydraulic microdrive controlled by a stepping motor. Recordings typically were multiunit (for advantages of multiunit mapping procedures, see Kaas[7]), and were conventionally amplified and displayed.

In each experiment, a large sector of somatosensory cortex was mapped. Extensive overlap of the mapped sectors from the 6 animals allowed basic features of all parts of the maps to be checked in two or more monkeys, and permitted the construction of a composite summary from highly detailed regional maps in 4 monkeys (Fig. 1). Electrode penetrations were made approximately 250–300 μm apart. Number of recording sites per animal ranged from 263 to 670. In depth penetrations down the posterior bank of the central sulcus (Fig. 3), or down the medial wall of the cerebral hemisphere (Fig. 4), recording sites were examined every 250 μm, often to depths of 7 mm or more. At selected locations in electrode penetrations, small electrolytic lesions were placed by passing DC current (10 μA, 5 s). These lesions were used to relate physiological results to cortical architecture. Cutaneous receptive fields for recording sites were defined as the skin region from which a distinct response was obtained with very light tactile stimulation with fine hand-held probes. For hairy skin, receptive fields were typically defined as the region where moving hairs without visibly distorting the skin evoked neural activity. For glabrous skin, receptive fields were defined as the region where just visible indentation of the skin with the probe produced a response. At the end of the experiment, the animals were deeply anesthetized and perfused with fixative. The brains were later cut in the sagittal plane, and sections were stained

for Nissl substance with cresylecht violet or for myelin with hematoxylin.

RESULTS

Microelectrode mapping methods were used to determine the organizations of the representations of the body surface in Areas 3b and 1 of six cebus monkeys. Conclusions were based on over 3000 recording sites in Areas 3b and 1, and the immediately adjacent parts of Areas 3a and 2. Most of the findings were very similar to those reported elsewhere for owl monkeys[12], macaque monkeys[15], and squirrel monkeys[19]. Thus, Area 3b and Area 1 each appeared to contain a separate and complete representation of the body surface. All recording sites in both fields were activated by cutaneous stimuli. The two representations were in parallel, proceeding from the tail in cortex on the medial wall of the cerebral hemisphere, to the oral cavity in lateral cortex along the Sylvian fissure. The two representations were roughly mirror-images of each other.

In addition, cortex rostral to Area 3b and caudal to Area 1 was predominantly activated by stimulating deep body receptors. Because these observations are similar to those made for other monkeys, they are only briefly described and they are not documented in detail. Instead, the description concentrates on two unusual features of the two cutaneous representations in cebus monkeys. The most significant observation is that the representations of at least some parts of the hairy body surface were reversed in orientation in both Areas 3b and 1 of cebus monkeys as compared to macaque and owl monkeys. This reversal was similar to that found in the closely related squirrel monkey. The other unusual feature of somatosensory cortex of cebus monkeys was the greatly expanded representation of the tail, which is prehensile and an important tactile organ in cebus monkeys.

An overview of the representations

The basic features of the two representations in Areas 3b and 1 are shown in Fig. 1. All parts of the two representations were remapped and found to be similar in at least two experiments, and many parts of the two representations, including cortex devoted to the trunk, were found to be similar in 4 different experiments. However, since there was minor variability from case to case, it could be misleading to 'average' data. Thus, Fig. 1 is a composite of results from 4 experiments, with mediolateral segments of the maps based completely on single cases. Much of Area 3b and a portion of Area 1 are buried in the cortex of the posterior bank of the central sulcus so that a surface view of the brain (Fig. 1A) shows much of Area 1, but little of Area 3b. Thus, the details of the two representations are shown on a two-dimensional view with the portions of Areas 3b and 1 on the posterior bank of the central sulcus and on the medial wall of the cerebral hemisphere 'unfolded'. A narrow strip of Area 3b extends onto the floor of the anterior bank of the central sulcus. This portion was difficult to reach with penetrating electrodes, and was largely unmapped. Therefore, the unfolded summary slightly underestimates the width of the Area 3b map. Limited recordings in cebus monkeys and more complete maps in other monkeys indicate that this unmapped fringe extends the representations of body parts located along the anterior margin of the unfolded summary map. The border between the Area 3b and Area 1 map corresponds to a reversal of somatotopic sequence as determined electrophysiologically and matches the architectonic change from characteristics of Area 3b to Area 1 as determined from serial parasagittal brain sections. The posterior border of Area 1 was determined architectonically, and it corresponds to a marked reduction and often a complete loss of responsiveness to cutaneous stimuli. The architectonic features of Areas 3a, 3b, 1 and 2 in cebus monkeys (also see ref. 2) are similar to those we have illustrated and described for owl[12], squirrel[19] and macaque monkeys[15].

In overall organization, the separate representations in Areas 3b and 1 were in parallel and roughly mirror-images of each other. The representations progressed from cortex on the medial wall of the cerebral hemisphere that was devoted to the tail, to the posterior leg, foot, ante-
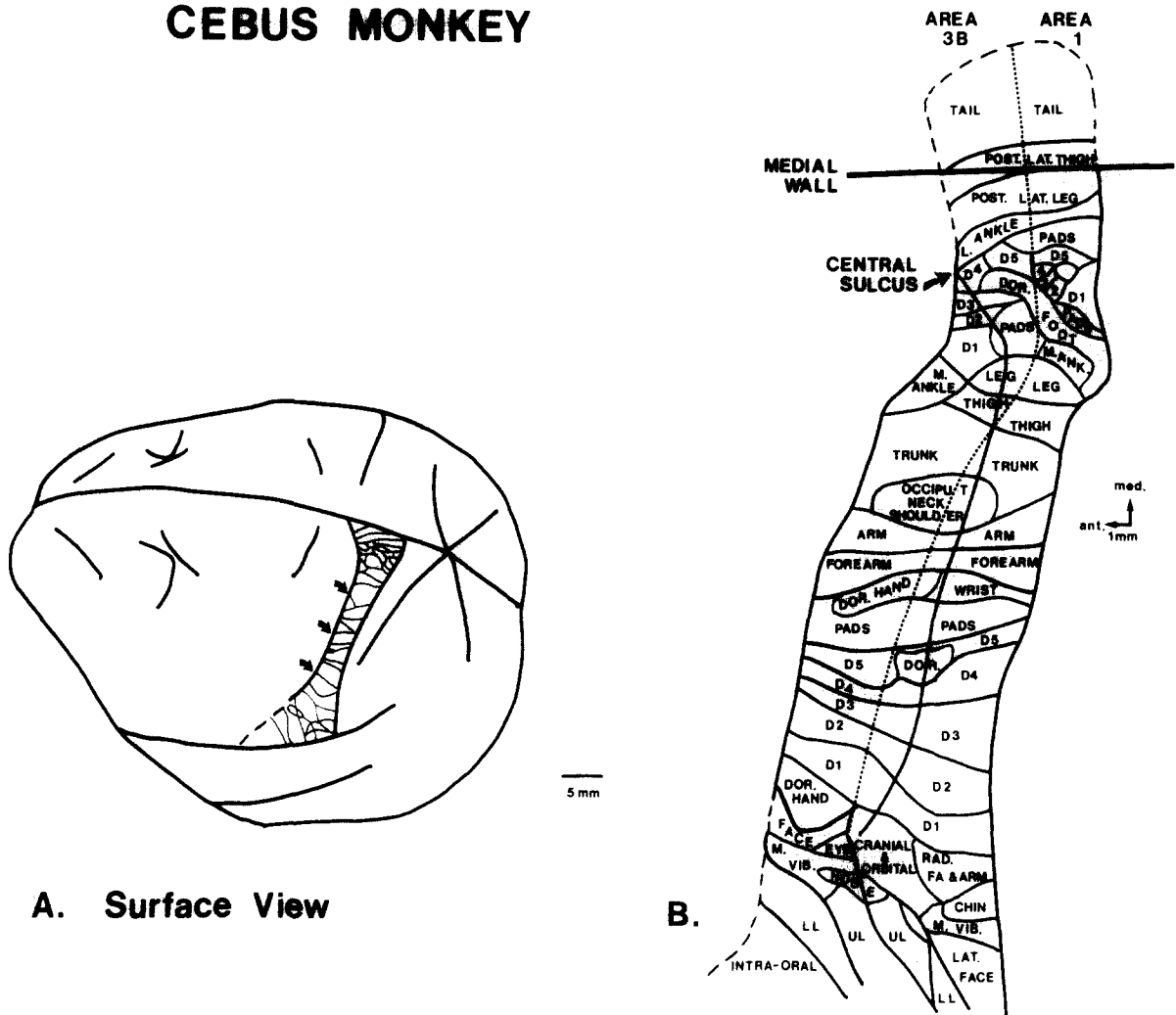
CEBUS MONKEY

A. Surface View

B.

Fig. 1. Location and organization of Areas 3b and 1 of cebus monkeys. A: dorsolateral view of cebus brain indicating the location of the cutaneous representations of Areas 3b and 1 of somatosensory cortex. The arrows indicate that the majority of the map in that region is buried deep in the central sulcus. Thus only some of Area 1 is visable in this region. Area 3b reaches the exposed surface in regions medial and lateral in cortex. B: somatotopic organization of Areas 3b and 1 of cebus S-I as revealed by a composite map derived from 4 individual regional experiments and superimposed using overlapping regions to form a composite (see text for additional details). The location of the border between Areas 3b and 1 is indicated by a dashed line. The central sulcus and medial wall are indicated by heavy solid lines. Note the double representation of the body surfaces which form approximate mirror-images of each other. While the two fields are organized roughly in parallel there are differences in the two representations.

rior leg, trunk, occiput, arm, hand, face and finally to the oral cavity in the most lateral cortex. The existence of two separate maps can be partially appreciated by noting the spatially separate anterior and posterior locations of some body parts such as the digits of the foot and the mystacial vibrissae in the summary map, but further support of this conclusion depends on a

detailed consideration of receptive field sequences, such as those shown in Figs. 2 and 3, that demonstrate the roughly mirror-image replications of restricted body parts. In Fig. 2, for example, it can be seen that the representation of the glabrous digit 4 was represented from tip to base in a rostrocaudal sequence in Area 3b and a caudorostral sequence in Area 1. A similar
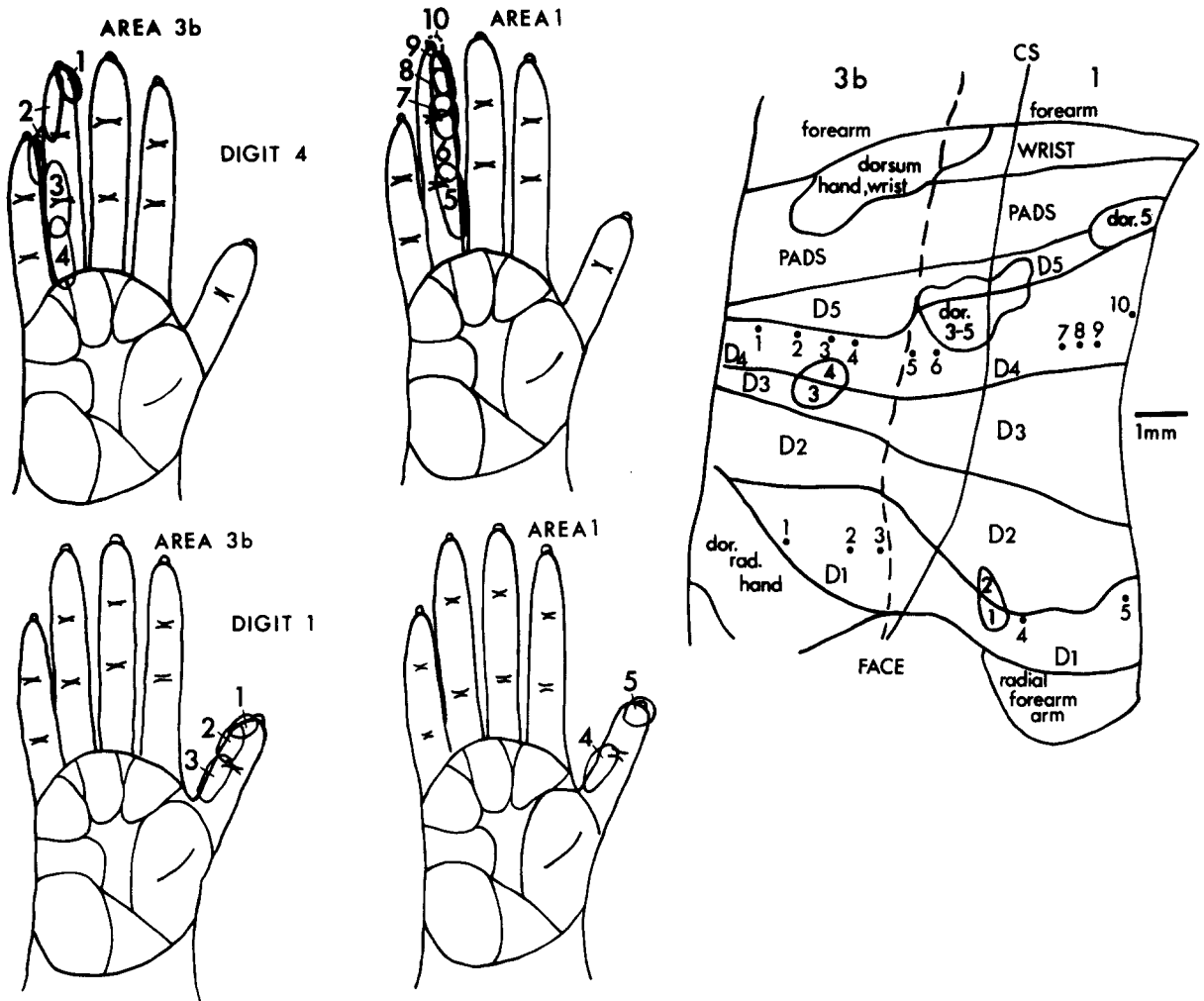
Fig. 2. Representation of the glabrous hand digits in Areas 3b and 1. This figure illustrates two rows of penetrations which cross Areas 3b and 1 from rostral to caudal. The first row crosses the digit 4 representations, and receptive field locations progress from the distal digit rostral in Area 3b (fields 1 and 2) to the proximal digit (field 4) at the caudal border of Area 3b. The sequence of receptive fields reverses at the border and recording sites extending from rostral Area 1 to caudal Area 1 demonstrate receptive fields whose locations shift from the proximal digit (field 5) to the digit tip (fields 9 and 10). A similar sequence of receptive fields is indicated for a row of recording sites which extended across the width of the digit 1 representations. Thus recording sites located rostrally in Area 3b and caudally in Area 1 had receptive fields located on the distal digit, while recording sites near the 3b/1 border had receptive fields on the proximal digit.

reversal is shown for digit 1. Opposite rostrocaudal sequences with a reversal at the base of each digit characterized all representations of the glabrous digit surfaces. The digits of the foot were similarly organized so as to point in roughly opposite directions in the two fields.

It is also important to emphasize that the two representations were not identical. Most notably, a representation of the radial forearm and arm was found lateral to the representation of the hand in Area 1, but not in Area 3b. There were also differences in the two representations in where the dorsal surfaces of the digits were located, in the proportions of the anterior leg and thigh represented in cortex lateral to the foot, and in many details of the somatotopic order of the face parts.

As is apparent in Fig. 1, the summary map is incomplete laterally. Parts of Areas 3b and 1 extend onto the dorsal bank of the Sylvian fissure, and these parts were not mapped. The Area 3b map is more complete. We estimate from re-

cording in owl and squirrel monkeys that the representations of the teeth and tongue occupy somewhat more cortex than the region indicated by 'Intraoral' in Fig. 1, and this would complete the map. More of the Area 1 map, including all of the representation of the teeth and tongue, is missing.

The reversed representations of the trunk

Receptive fields for progressions of recording sites that crossed the 'unfolded' map from rostral to caudal clearly revealed that the ventral midline of the trunk was represented rostrally in Area 3b and caudally in Area 1, while the dorsal midline of the trunk was represented at the 3b/1 border. Receptive fields for a typical row of recording sites are shown in Fig. 3, both as placed on the unfolded map, and in their actual locations in the folds of the central sulcus and on the surface of the brain. For the unfolding, all recording sites were orthogonally related to cortical layer IV. Near the 3a/3b border in the depths of the central sulcus in the actual brain or 'rostrally' in the unfolded map, receptive fields for recording sites were along the ventral midline of the body (see recording site and receptive field no. 1; receptive fields for the indicated recording sites just dorsal to no. 1 were very similar to no. 1). In the progression of recording sites to the 3b/1 border, receptive fields gradually shifted across the contralateral trunk to the dorsal midline of the body (receptive field no. 5). In Area 1, the opposite sequence of representation was found so that receptive fields moved from the dorsal midline of the body to the ventral midline of the body in a rostrocaudal row of recording sites, 6–9. The pattern shown in Fig. 3 was found in all 4 cebus monkeys where the trunk representations in Areas 3b and 1 were explored. Thus, the rostrocaudal sequences of representation of the trunk in Area 3b and in Area 1 were reversed in cebus monkeys, as compared to owl[12] and macaque monkeys[15], but were identical to the sequences of representation in squirrel monkeys[19].

The reversed representation of body parts was not limited to the trunk in cebus monkeys, but involved parts of the limbs, shoulder, and occi-

put as well. These are parts of the body surface that appear to be represented together with the trunk as a single somatotopic pattern. Thus, the dorsal midline of the shoulder region, neck, and caudal head were found along the 3b/1 border adjacent to the dorsal trunk. Somatotopic continuity was also preserved near the 3b/3a and the 1/2 borders where the representations of the ventral chest were continuous with that of the ventral arm. More medially in the cortex, the representation of the dorsal midline of the caudal trunk at the 3b/1 border was continuous with that of the upper lateral thigh, while the medial thigh was found away from the border, rostrally in Area 3b and caudally in Area 1. Thus, it appeared that the representations of all hairy skin surfaces that were located between the representations of the hand and foot were reversed in orientation in Areas 3b and 1 of cebus monkeys as compared to owl and macaque monkeys.

The enlarged representation of the tail

The prehensile tail of the cebus monkey is actively used in tactile exploration and the skin surface of the tail has a greatly enlarged cortical representation in comparison with owl, squirrel and macaque monkeys, where the tail is not such an important tactile organ. The region of cortex that is activated by light touch on the tail was extensively explored in 3 cebus monkeys. The cortex devoted to the tail was on the medial wall of the cerebral hemisphere adjoining cortex related to the posterior thigh and gluteal region. In electrode penetrations down the medial wall, it was possible to obtain sequences of receptive fields for successively deeper recording sites that progressed from the posterior lower leg and ankle, for cortex on the dorsomedial surface, up the posterior leg to the base of the tail, and down the tail to the tip for the deepest recording sites. The receptive fields were large enough to cover most or all of the width of the tail, and therefore rostrocaudal sequences of recording sites revealed no clear pattern of receptive field sequences.

A typical receptive field sequence for successive recording sites down the cortex of the medial wall is shown in Fig. 4. The sequence shows
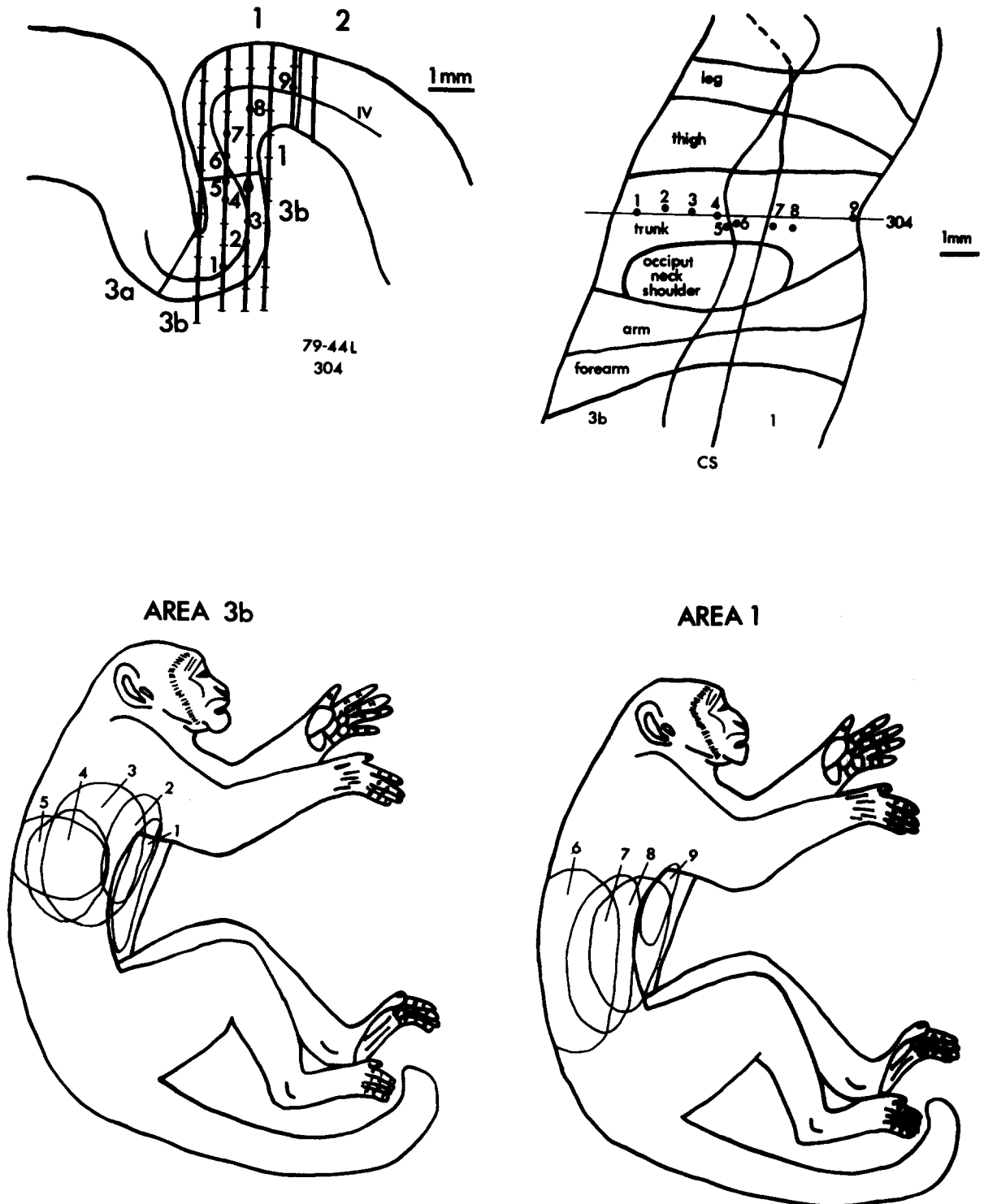
Fig. 3. Organization of the representations of the trunk. At the top left is illustrated a parasagittal section showing a row of recording sites derived from several depth penetrations down the posterior bank of the central sulcus in the region of the mid-trunk representation. Recording sites 1–9 were chosen from many available sites (indicated by hatch marks) to illustrate receptive fields for neurons close to layer IV. At the top right is illustrated the cortical map derived from this mapping experiment and indicates the approximate location of the section illustrated on the left and illustrates the locations of recording sites in the 'unfolded' map. Below are indicated the receptive fields corresponding to the recording sites illustrated above. The ventral trunk is represented rostrally in Area 3b and caudally in Area 1 while the representation of the dorsal trunk in found at the 3b/1 border.

that the representation of the tail was continuous with that of the posterior thigh, and that the largest receptive fields were for the base of the tail, while smaller receptive fields were for the tip of the tail. In the depths of other penetrations (not shown), recording sites were obtained with even smaller receptive fields on the tip of the tail of approximately one-fourth the size of receptive field no. 12 in Fig. 4.

The somatotopic organization and extent of the tail representation is further illustrated in Fig. 5 from data taken from another monkey. In this case, 10 depth penetrations were made down the medial wall of the cerebral hemisphere through the representations of the lateral foot, posterior hindlimb, and tail. Receptive fields

were determined approximately every 500 μm, with some penetrations remaining in responsive cortex for 7 mm or more. Compared to the case illustrated in Fig. 4, the somatotopic map represented in Fig. 5 was shifted medially so that parts of the foot were on the medial wall. By schematically dividing the tail into 4 sectors along its promimal-distal extent, it can be seen from Fig. 5 that the somatotopic progression in every electrode penetration was from proximal to distal.

In Fig. 5, the posterior electrode penetrations did not reach cortex activated by the tip of the tail, and this was probably a result of the electrode angle. In addition, because of the spacing of electrode penetrations, it was difficult to de-
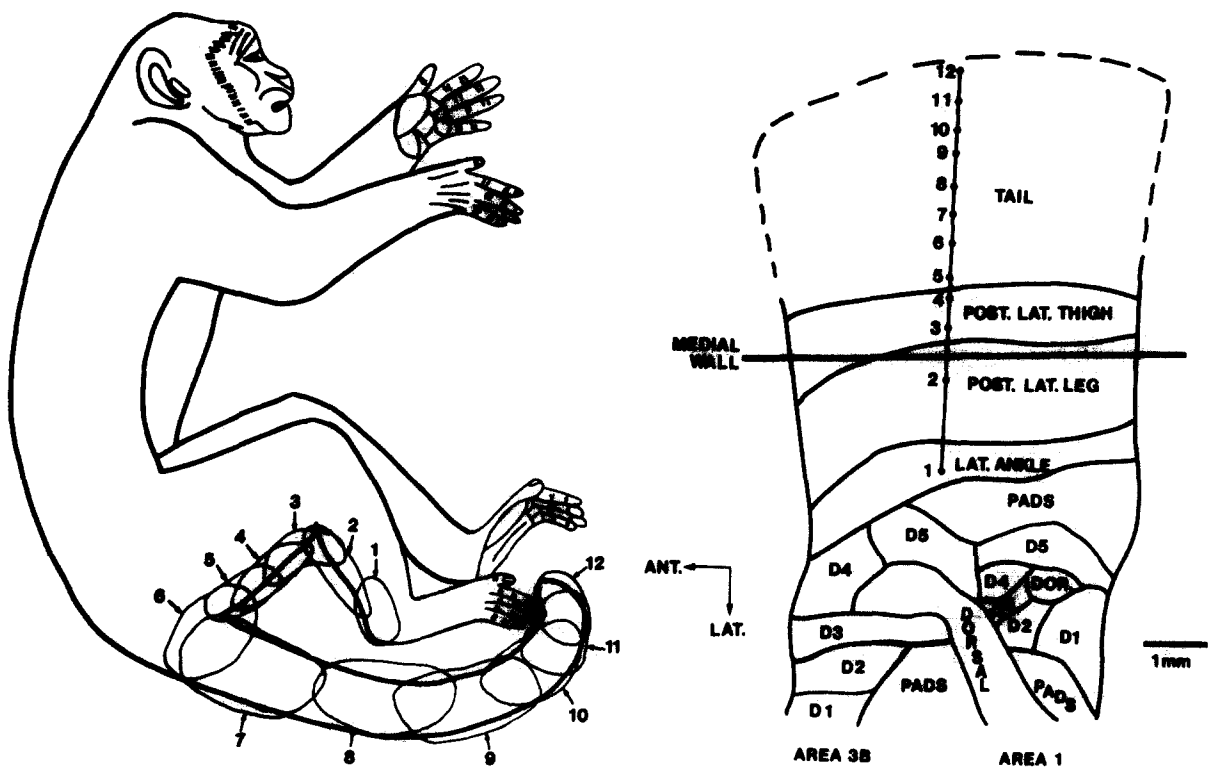

Fig. 4. Representation of the posterior hindlimb and tail. This figure illustrates a row of recording sites (1–12) extending from the dorsal surface of medial cortex down the medial wall of the hemisphere. The corresponding receptive fields are illustrated on the 'Cebus' figure at the left. This row of recording sites demonstrates a single topographic sequence of the posterior margin of the ankle, leg and thigh, as well as the proximal-distal sequence of the representation of the tail. This row of recording sites falls approximately along the Area 3b/1 border. Since receptive fields tended to be large except near the tip of the tail, and the body parts are relatively small, we were unable to demonstrate two distinct maps of the posterior hindlimb and tail monkey.

termine precisely the rostral and caudal borders of the responsive region. In addition, the amount of cortex devoted to the tail was difficult to estimate accurately, since the lack of responsiveness in a depth penetration could simply result from the electrode angling away from the responsive layers of cortex. In Fig. 4, for example, the cortex devoted to the tail could have extended somewhat deeper than recording site no. 12 since the recording sites with small receptive fields on the tip of the tail were not yet detected. Given these limitations, the cortical representations of the tail were estimated to be 12 mm² in one monkey and 18 mm² in another monkey. Both estimates are conservative, and probably 20 mm² or so of cortical surface is actually de-

voted to the tail in Areas 3b and 1 of cebus monkeys.

It was not possible to clearly reveal two separate somatotopic representations of the tail, one for Area 1 and one for Area 3b. Since the dorsal to ventral progression in cortex was from the representation of the base to the tip of the tail, the expected rostrocaudal representational sequences across Areas 1 and 3b would be around the contralateral circumference of the tail. Receptive fields were too large to reveal such progressions of receptive fields in the tail. Yet, it was obvious that parts of the tail represented in Area 1 were also represented in Area 3b. Thus, the principle of separate parallel representations of body parts in Areas 3b and 1 was upheld for the
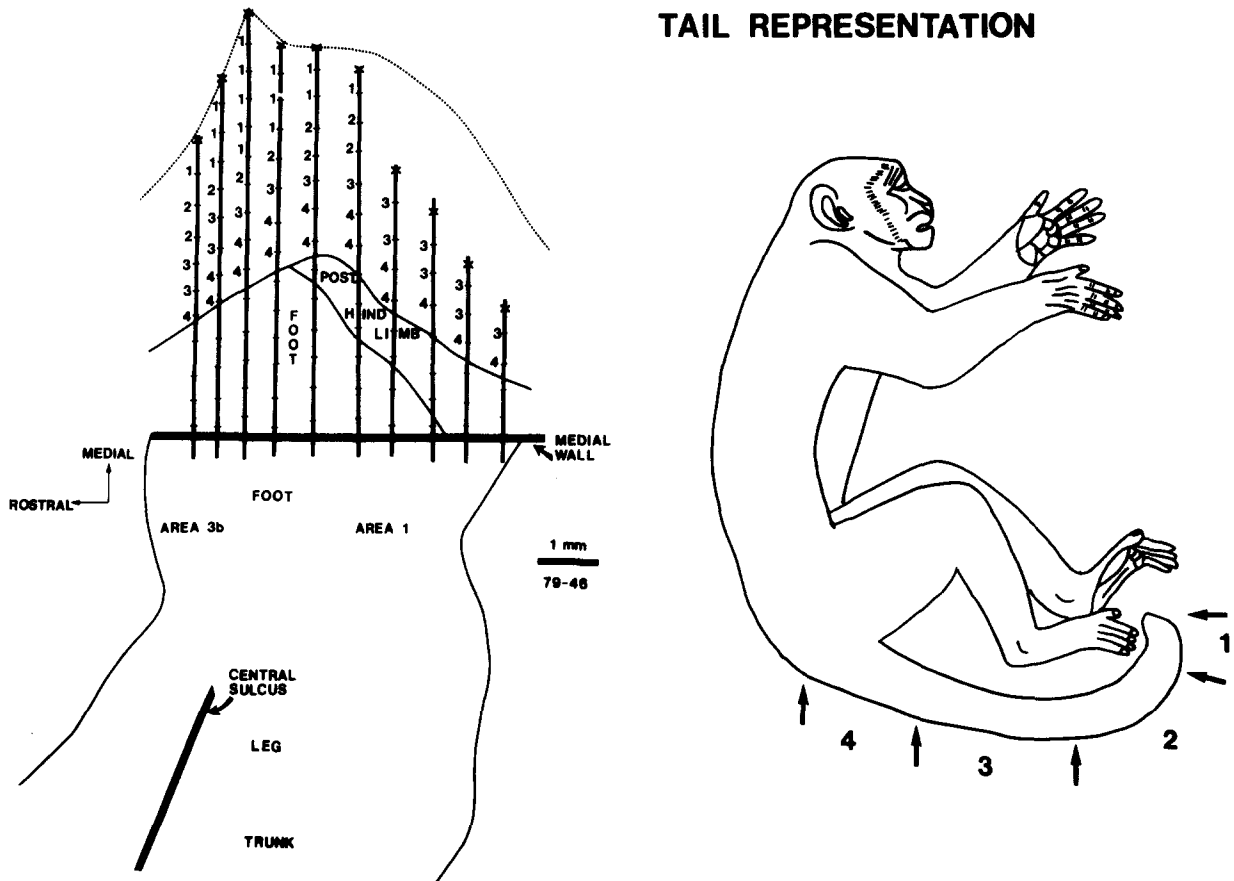
CEBUS MONKEY

TAIL REPRESENTATION

Fig. 5. Organization and extent of the tail representation. The tail of the 'Cebus' monkey is schematically divided into 4 sectors in the figurine on the right. Receptive fields located on the tail were assigned one of these 4 sector designations and these labels are presented on the two-dimensional "unfolded" map at the left. The dashed line indicates our best estimate of the ventral extent of the tail representation, while an X marks the first unresponsive recording site in each penetration.

tail, but data clearly supporting the concept of mirror-reversals was not obtained.

DISCUSSION

The present results demonstrate in a fourth genus of monkeys that Areas 3b and 1 each contain separate complete or largely complete parallel and roughly mirror-image representations of the body surface (for a recent alternative concept of somatosensory cortex organization, see ref. 11a). The locations of given body parts in the two representations were specified in some detail, for comparison with similar results in other monkeys, and as a guide for future studies in cebus monkeys. The Area 3b and Area 1 maps in owl monkeys, cynomolgus macaque monkeys, and squirrel monkeys have been extensively discussed and related to other electrophysiological and anatomical studies elsewhere[7,9-13,15]. The present discussion is limited to 3 unusual features of organization noted in the two cutaneous cortical fields of cebus monkeys: the reversed orientation of some body parts in both representations, the split representation of the arm in Area 1, and the greatly expanded representation of the tail.

The major goal of the present experiments was to determine the orientation of the body parts in the Area 3b and 1 representations to see if some were reversed as in squirrel monkeys. Our previous microelectrode mapping studies in New World and Old World monkeys revealed two basic organizational schemes. Both schemes share a common orientation of the glabrous digit representations for both the hand and foot. The digits 'point' roughly rostrally in Area 3b and caudally in Area 1. The trunk, anterior hindlimb, and posterior forelimb are represented in a somatotopically continuous manner as a 'block'[18] between the hand and foot representations. It is this trunk-limb block that is reversed in squirrel monkeys as compared to owl and macaque monkeys. Thus, in both owl and macaque monkeys, the dorsal midline and outer skin surfaces of the limbs are represented at the rostral extreme of Area 3b and the caudal extreme of Area 1, with the ventral midline and the

inner limb surfaces at the border between the two areas. In squirrel monkeys, the ventral midline of the trunk and inner limb surfaces are represented rostrally in Area 3b and caudally in Area 1, while the two representations are joined along the dorsal midline of the trunk. The present results show that this middle trunk-limb representational block is reversed in cebus monkeys as it is in squirrel monkeys.

The somatosensory cortex in cebus monkeys was investigated to determine if cebus and squirrel monkeys show the same organizational scheme. Comparisons of squirrel and owl monkeys already indicated that all New World monkeys do not share a common plan. Therefore we speculate that at some point in the evolution of New World monkeys, a split occurred with one phylogenetic line, including owl monkeys, having the basic plan, and a second line, including squirrel monkeys, having the plan with the reversed trunk-limb block. We now know that cebus monkeys also have a reversed trunk-limb block. Since it is unlikely that brain organization changed independently twice in the same way in New World monkeys, the present results support the argument that the change occurred before the *Cebus-Saimiri* divergence, but after the earlier divergence that led to *Aotus*. While the phylogenetic taxonomy of New World monkeys is a matter of debate, a close *Cebus-Saimiri* relationship has often been postulated (e.g. refs. 3, 5, 14 and 17), and the present results support that proposition. Furthermore, we suggest that the reversed somatotopic block in some New World monkeys can be used as a taxonomic tool in classifying other New World monkeys. Based on current phylogenetic classifications, we would predict that the somatosensory cortex in *Callithricidae* corresponds to the general plan found in *Aotus*, while the organization found in *Ateles* and *Alouatta* may be either that of the specialized type found in *Saimiri* and *Cebus* or the general plan of *Aotus*.

The partial representation of the radial arm and forearm in cortex lateral to that representing the hand in Area 1 but not Area 3b of cebus monkeys is another interesting feature of somatotopic organization. Such a split representation

of the forearm is a common feature of primary somatosensory cortex, S-I, of non-primates, which we regard as the homologue of the Area 3b representation in monkeys[8], and it is a feature of S-I in prosimians[18]. However, it was not found in owl monkeys, squirrel monkeys or macaque monkeys, and it was not noted in a microelectrode mapping study of somatosensory cortex in spider monkeys, *Ateles*[16]. We have argued elsewhere[18,19] that the split forearm is a primitive feature of Area 3b organization stemming from a configuration, seen now in S-I of nonprimates[8], where the overall continuity of the representation was maintained by the 'split' parts of the forelimb representation connecting caudally behind the representation of the hand. As a consequence of the great enlargements of the representations of the glabrous hand and foot in primates, the extent of the continuity in the overall maps has been greatly reduced where the body parts join other body parts in Areas 3b and 1. It may be that this reduction in continuity made the reversal of the trunk-limb block of somatosensory cortex possible[19]. The representation of a portion of the forelimb lateral to that of the hand in cebus monkeys, we feel, is a reflection of a more primitive condition. It is interesting that this split is found in Area 1, which apparently evolved after Area 3b (S-I)[8] and as a mirror-duplication of Area 3b[7].

The final point of discussion is the enlarged representation of the tail in Areas 3b and 1 of cebus monkeys. Unlike squirrel monkeys, owl monkeys and macaque monkeys, the cebus monkey uses its tail for active tactile exploration.

From the pioneering studies of Adrian[1] and Woolsey[20], it has been apparent that structures that are important sensory surfaces have enlarged cortical representations. In a previous evoked potential study of somatosensory cortex in cebus monkeys, approximately 30 mm^2 of cortex appeared to be devoted to the tail in cebus monkeys[6]. Our present estimate is that about 20 mm^2 of cortex in Areas 3b and 1 are activated by stimulating the tail. The difference in estimates probably relates to the fact that evoked potential studies can slightly overestimate sizes of representations due to current spread, and that the region of cortex related to the tail explored by Hirsch and Coxe probably included portions of Areas 3a and 2, as well as Areas 3b and 1. The present results indicate that in proportion to cortex, the tail occupies about as much tissue as the foot in Areas 3b and 1 of cebus monkeys. For either the tail or the foot, this corresponds to approximately 10% of the mapped cortex summarized in Fig. 1. This proportion is roughly similar to the estimate of 16% of 'S-I' made for the tail representation of the spider monkey[16], which also has a prehensile tail. In contrast, the representations of the tail are an order of magnitude less in size than that of the foot in owl, squirrel and macaque monkeys[12,15,19] where the tail is not used in tactile exploration.

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